THE INFLUENCE OF LIGHT IN THE DEPTH REGULATION
OF CRAB LARVAE [1]

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Light has been described as the principal environmental factor controlling the vertical distribution of planktonic animals (see *e.g.*, Bainbridge, 1961; Thorson, 1964). Previously, the author has demonstrated that responses of larvae of two Xanthid crabs, *Leptodius floridanus* (Gibbes) and *Panopeus herbstii* Milne-Edwards, to gravity and hydrostatic pressure provide a depth regulatory mechanism in the absence of light (Sulkin, 1973).

In this study, experiments were conducted to determine the photic responses of larvae of the same two species. The results of these experiments and an assessment of the influence of light on depth regulation are presented here.

MATERIALS AND METHODS

Ovigerous specimens of *L. floridanus* were obtained commercially throughout the year from Florida; ovigerous specimens of *P. herbstii* were collected along rock jetties and oyster shoals near Beaufort, North Carolina, from May until October.

Both species have four zoea stages and one megalopa. Rearing conditions were chosen on the basis of work done on *P. herbstii* by Costlow, Bookout and Monroe (1962). A temperature of 25° C and a salinity of 25‰ were selected as the combination best suited for successful development in both species. Larvae from each female were kept in mass culture in several large finger bowls. Cultures were maintained in constant temperature cabinets with a photoperiod of 12 hours of light. Larvae were transferred daily to clean bowls of filtered seawater and fed freshly-hatched *Artemia salina* nauplii.

To study photic responses, a sample of larvae was pipetted into an observation tank, which was then sealed and inserted into one of the two observation compartments in the control cabinet illustrated in Figure 1. The interior of the compartment was lined with styrofoam, painted flat black. The light source, a 150 W incandescent bulb, could be positioned at either end of the tank and aimed along its axis. A sheet of ground glass was inserted between the bulb and the observation compartment to diffuse the light. To eliminate the possibility of a temperature gradient, the observation compartments were insulated from the light sources by two Plexiglas plates, separated by an air space. A dim red back-light behind the observation compartments silhouetted the larvae. The entire cabinet could be positioned vertically, as shown in Figure 1, or horizontally.

The observation tank was constructed of 1.2 cm thick transparent Plexiglas, measuring 61 cm long with an internal cross sectional area of 6.45 cm². Based
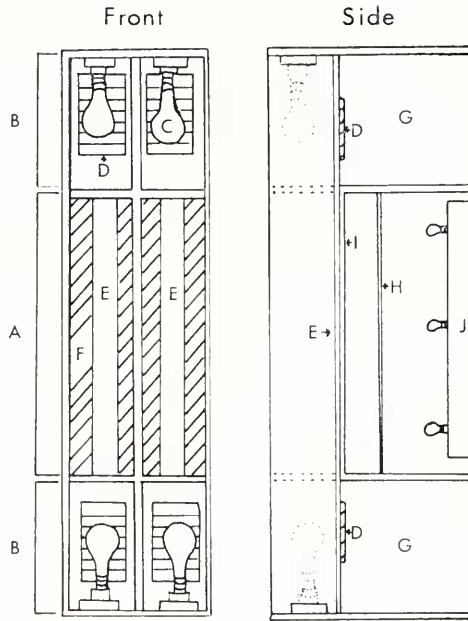
FIGURE 1. Light cabinet (figure not drawn to scale): A. chamber for observation tank; B. light chamber; C. light bulbs; D. ventilation outlets; E. red back-light window; F. styrofoam insulation; G. rear dead space ventilation area; H. frosted glass; I. red filter; J. backlight source.

upon published values for oxygen consumption of zoea and megalopa larvae (Vernberg and Costlow, 1966), the volume of the tank (500 ml) should have been sufficient to provide ample oxygen for the number of larvae used and the duration of the observations. Indeed, there was no observed change in behavior during the course of the experiments which could be attributed to oxygen deficit.

Specific details for each experiment are described with the results.

RESULTS

Orientation to light

Light, at an intensity of 10 foot-candles (ft.-c), was aimed along the axis of the observation tank from one end. The tank was positioned horizontally so that gravity responses were isolated from those of light.

Figure 2 illustrates the primary orientations assumed by zoeae of all stages. Of the two primary orientations observed, that illustrated in Figure 2A was most common. When movement begins, the rostral spine and antennae are pointed down and away from the light. The dorsal spine is pointed toward the light with its main axis at an angle approximately 30° above the horizontal plane. The abdomen remains flexed. This orientation is accompanied by prolonged bursts of swimming.

In the other primary orientation (Figure 2B), movement proceeds backward, with the eyes facing away from the light and the rostral spine and antennae pointed
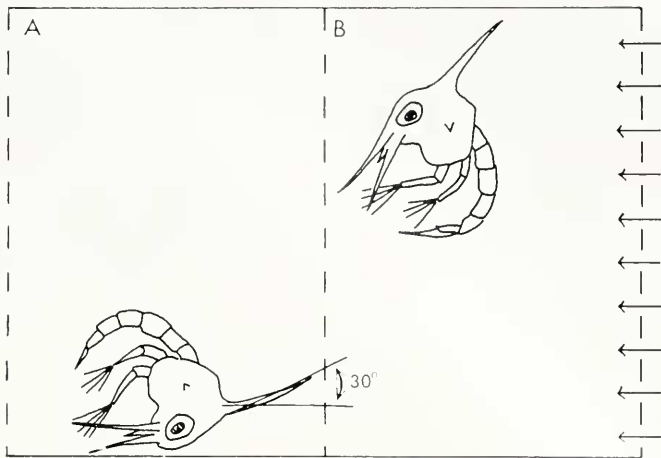
FIGURE 2. Orientation typical of zoea stages in horizontal light (light is coming from the right of the diagram as indicated by the arrows; the figure is not drawn to scale) : A. position most frequently observed in horizontal light; B. position occasionally observed (see text for details).

down. The dorsal spine is held upright. The abdomen does not remain flexed, but flicks periodically. This behavior may be stimulated by a tendency to sink, since larvae assuming this orientation characteristically were located at the top of the horizontal tank.

The megalopa swims by the use of pleopods located on the extended abdomen. Periods of inactivity or slow crawling are interrupted by a "jump" up into the middle of the tank, followed by a series of looping movements which carry the megalopa toward the light.

Secondary orientation in response to light was tested in the following manner. Samples of each zoea stage and the megalopa of *L. floridanus* were placed in each of two horizontal observation tanks and allowed to disperse in darkness (dim red back-light). After 1 hour, light (10 ft.-c) was aimed along the axis of one of the tanks from one side. Larvae in the other tank remained in darkness. At intervals shown in Table I, the number of larvae in the half of the tank nearest the light source were counted, as were those in one half of the control tank (chosen at random). Results of repeated tests for each stage are shown in Table I as percent of total sample. In all four zoea stages and in the megalopa, net movement was toward the light (positive phototaxis).

A similar experiment was conducted on the first and fourth (last) zoea stages and the megalopa of *P. herbstii*. Based on the results with *L. floridanus*, a control was not deemed necessary. The results are shown in Table II. Again, net movement was toward the light (positive phototaxis).

Responses to changes in light intensity

The response of zoea larvae to various light intensities was measured in the following manner. A sample of larvae was pipetted into the observation tank which

TABLE I

Leptodius floridanus: *the per cent of total sample in half of observation tank nearest light source (experimental) or in randomly chosen half of tank in darkness (control) at specified time intervals.* (N = *total number of larvae tested in each case.*)

Stage of development	N		Time (min)										
			0	2	4	6	8	10	20	30	40	50	60
Zoea I	177	Control	51	50	50	50	53	53	50	51	50	47	50
	172	Experimental	49	78	84	88	90	90	92	94	94	93	93
Zoea II	57	Control	50	53	53	53	51	51	51	53	53	47	51
	59	Experimental	49	88	95	97	95	93	97	97	97	92	93
Zoea III	59	Control	51	54	51	53	51	47	51	56	49	49	49
	56	Experimental	48	86	91	91	93	95	96	93	96	95	95
Zoea IV	60	Control	50	45	45	43	43	47	47	45	47	47	48
	100	Experimental	49	86	93	95	96	95	96	96	95	94	94
Megalopa	45	Control	53	53	47	47	40	40	47	53	47	47	47
	45	Experimental	51	56	62	64	71	73	78	82	82	84	89

was then placed in the light-temperature cabinet in the horizontal position. The larvae were attracted to one end of the tank by a dim light. A light of known intensity was then aimed along the axis of the tank from the opposite end. As the larvae swam toward it, individuals were timed as they traversed a 10 cm long space marked off in the middle of the tank. Larvae pausing for more than 2 seconds were discounted. At each light intensity 50 individuals of *L. floridanus* (Stage I and Stage IV) and 30 of *P. herbstii* (Stage I) were timed. Swimming speed was calculated in cm/sec.

Four light intensities were tested. As measured by an irradiance meter at the end of the tank nearest the light source, they were 10 ft.-c, 30 ft.-c, 50 ft.-c, and 70 ft.-c. Higher intensities could not be tested in the apparatus because of the heat produced. Diminution of intensity along the 10 cm observation interval was negligible.

Data for each species or stage was subjected to the formal test of linearity (Li, 1964). Although the data from all three showed linearity, only in the first zoea stage of *P. herbstii* was the slope of the regression significantly different from

TABLE II

Panopeus herbstii: *the per cent of total sample in half of the observation tank nearest light source at specified time intervals.* (N = *total number of larvae tested in each case.*)

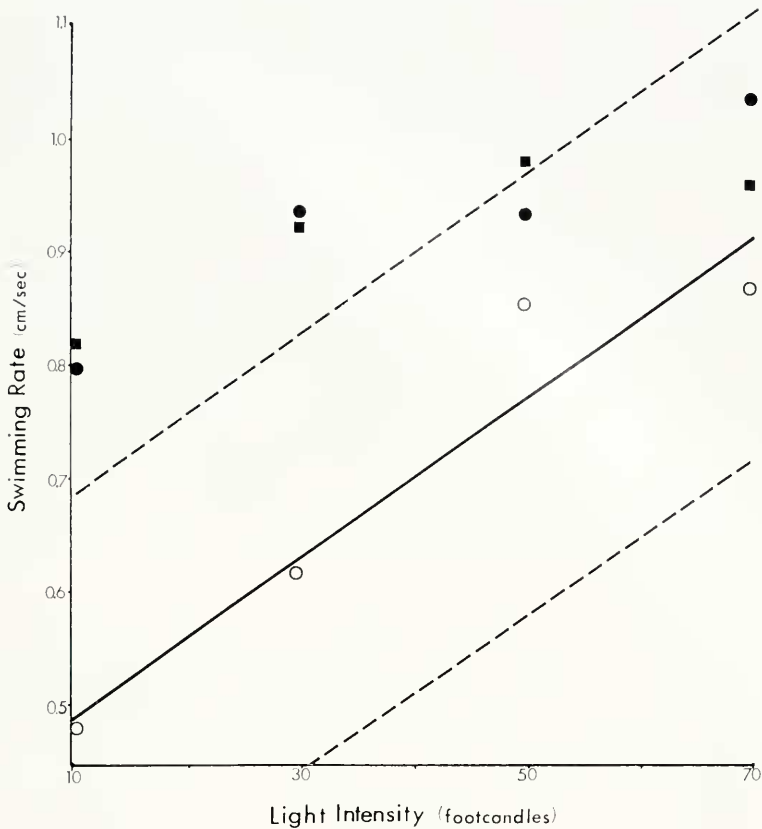| Stage of development	N	Time (min)										
		0	2	4	6	8	10	20	30	40	50	60
Zoea I	176	48	85	83	82	85	87	91	82	82	83	85
Zoea IV	96	49	77	81	85	83	87	90	92	89	91	93
Megalopa	52	50	52	58	62	64	70	74	74	74	81	81

FIGURE 3. Regression of swimming rate as a function of light intensity in the first zoea stage of *P. herbstii*. The two parallel dashed lines represent one standard error to either side of the solid regression line. The points indicate mean swimming rates measured for each larval stage at each light intensity (*P. herbstii*, Stage I: open circles; *L. floridanus*, Stage I: solid circles; *L. floridanus*, Stage IV: solid squares.)

zero ($P < 0.025$). The line of regression and standard errors are shown in Figure 3. An increase in swimming rate with an increase in light intensity is clearly indicated in this stage. Although both the first and fourth zoea stages of *L. floridanus* showed slight increases in swimming rate with an increase in light intensity, the slopes were not statistically significant (Stage I = $0.05 < P < 0.10$; Stage IV = $P > 0.25$). The mean swimming rates for *L. floridanus* ranged from 0.80 to 1.04 cm/sec (Stage I) and from 0.82 to 0.97 cm/sec (Stage IV); mean swimming rates for *P. herbstii* (Stage I) ranged from 0.48 to 0.86 cm/sec (Fig. 3).

Vertical distribution in light from above

Samples of each zoea stage and the megalopa were placed in each of two horizontal observation tanks and allowed to disperse in darkness (dim red back-light). After 1 hour, the tanks were rotated slowly to the vertical position, and the number

TABLE III

Leptodius floridanus: *the per cent of total sample in the upper half of the observation tank at the specified time intervals during "lighted tank" experiments. Italicized values are those measured in the "dark tank" experiments. These values were taken from Sulkin, 1973, Table I, page 76. (N = total number of larvae tested in each case.)*

Stage of development	N	Time (min)										
		0	2	4	6	8	10	20	30	40	50	60
Zoea I	172	51	70	77	78	74	74	64	66	61	55	56
	181	*53*	*60*	*60*	*62*	*58*	*60*	*57*	*50*	*47*	*54*	*57*
Zoea II	52	50	58	60	63	69	71	65	63	63	71	69
	59	*49*	*29*	*24*	*27*	*27*	*29*	*34*	*37*	*41*	*41*	*42*
Zoea III	92	51	62	72	74	73	70	66	73	67	71	73
	99	*49*	*32*	*30*	*33*	*39*	*38*	*38*	*37*	*40*	*41*	*38*
Zoea IV	98	51	62	58	55	58	60	55	52	53	55	54
	98	*49*	*28*	*19*	*19*	*18*	*20*	*17*	*18*	*22*	*17*	*16*
Megalopa	45	49	29	33	33	31	33	31	31	31	31	31
	44	*50*	*9*	*7*	*7*	*7*	*5*	*0*	*0*	*0*	*0*	*0*

of larvae in the upper half of each tank was counted (time = 0). Larvae in one of the two tanks were then subjected to light (10 ft.-c) aimed down the axis of the tank from above; the other tank remained in darkness. Numbers of larvae in the upper half of each tank were counted at prescribed intervals. The results of the "dark tank" experiment have been reported in detail elsewhere (Sulkin, 1973; see discussion).

The "lighted tank" experiment was conducted only on larvae of *L. floridanus*. Results of repeated tests for each stage are shown in Table III as per cent of total sample. ("Dark tank" values are included for comparison. The values, in italics, were taken from Sulkin, 1973, Table I, page 76.) In the lighted tank, the first zoea stage showed a net upward movement, with values ranging from a high of 78% at the six minute interval to a low of 55% at 50 minutes. The second and third zoea stages also showed a net upward movement, with values ranging from 71% to 58% and from 74% to 62%, respectively. The fourth zoea stage showed little net movement, with values ranging from 62% to 52%. The megalopa reached an equilibrium at 31% after 20 minutes.

In order to assess the impact of light on vertical distribution, the values obtained in the "lighted tank" were compared with those in the "dark tank" at the time of termination of both experiments (60 min). The per cent increase of the former over the latter is shown in Table IV. Light exerts a negligible effect upon

TABLE IV

Leptodius floridanus: *the per cent increase in values obtained in the "lighted tank" experiment over those obtained in the "dark tank" experiment at the 60 min interval.*

Zoea I	Zoea II	Zoea III	Zoea IV	Megalopa
−1.8	64.2	92.1	237.5	∞

the net vertical distribution of the first zoea stage, but substantially increases the per cent of total sample in the upper half of the tank in each of the succeeding larval stages.

These vertical distribution values represent equilibria, with frequent exchange of larvae between the upper and lower halves of the tank.

Relative influence of light and gravity as orienting stimuli

The zoea stages of *L. floridanus* and *P. herbstii* have been shown here to be positively phototactic and have been reported previously to be negatively geotactic (Sulkin, 1973). The influence of light and gravity can be opposed experimentally if a sample of larvae in a vertically positioned tank is subjected to light aimed up from below ("experimental"). The relative strengths of the two stimuli can be assessed by comparing the vertical distribution under the experimental conditions just described with that obtained when gravity alone is the stimulus. The latter condition can be simulated in a vertically positioned tank in darkness ("control"). After a 1-hour exposure to each of the two conditions, the number of larvae in the bottom quarter of each tank was counted. The pooled results of five independent tests are shown in Table V and are expressed as per cent of the total sample.

TABLE V

Percentages of first stage zoeae found in the bottom quarter after the sample has been subjected to either the control or the experimental conditions for one hour.   Total number of larvae subjected to each test are shown in parentheses.   Five independent tests were conducted in each case.

Stimulus	*L. floridanus*	*P. herbstii*
Control*	43 (N = 179)	7 (N = 165)
Experimental**	94 (N = 152)	99 (N = 164)

* Tank vertical, no light; gravity only taxis clue.
** Tank vertical, light from below; gravity and light taxis clues present and opposed.

A greater per cent of larvae was present at the bottom when light was aimed up from below than when gravity alone was the orienting stimulus. It can be inferred from this data that light response dominates that of gravity in a majority of the first stage zoeae of *L. floridanus* and *P. herbstii*.

Since the megalopa of *L. floridanus* and *P. herbstii* are both positively phototactic (as reported here) and positively geotactic (Sulkin, 1973), the stimulating influences of light and gravity are opposed in nature. This situation can be simulated experimentally by shining light down from above ("experimental"). The impact of light upon the vertical migration of megalopa can be tested by comparing results obtained in the "experimental" condition with those obtained using a vertical tank in darkness ("control"). The per cent of megalopa present in the bottom quarter of control and experimental tank are shown in Table VI.

The application of light aimed down from above stimulated only 30% of *L. floridanus* and 10% of *P. herbstii* to swim up from the bottom. It is apparent that

TABLE VI

Percentages of megalopa found in the bottom quarter after the sample has been subjected to either the control or the experimental conditions for one hour.   Total numbers of larvae subjected to each test are shown in parentheses.   Three independent tests were conducted in each case.

Stimulus	*L. floridanus*	*P. herbstii*
Control*	100 (N = 44)	100 (N = 50)
Experimental**	70 (N = 45)	90 (N = 50)

* Tank vertical, no light; gravity only taxis clue.
** Tank vertical, light from above; gravity and light taxis clues present and opposed.

the positive gravity response is dominant in a majority of the megalopa of both species.

DISCUSSION

The use of light in experimental studies of behavior of aquatic animals is a subject of considerable controversy. In his review of light as a factor influencing the distribution of invertebrate larvae, Thorson (1964) examined the question. He concluded that no standard rules for determining experimental light conditions were possible because light penetration is so heavily dependent upon local hydrographic conditions. The choice of experimental intensities is governed ultimately by the hydrographic conditions associated with the species' habitat and by limitations imposed by the experimental design.

Larvae of both *L. floridanus* and *P. herbstii* are likely to be found in estuarine and nearshore coastal areas. In his study of crab larval distribution in the Newport River Estuary near Beaufort, North Carolina, Pinschmidt (1963) reported mean secchi disc readings of from 0.28 m to 1.56 m. Readings generally were lowest during the spring and summer, the time of greatest abundance of brachyuran larvae. A mean value of 0.46 m can be calculated for the period between May and October at Pinschmidt's station 3, located midway along the salinity gradient in the lower Newport River. To estimate the depth reached by 1% of ambient radiant energy, secchi disc depth can be multiplied by a factor of 3.5 (Holmes, 1970). Thus only 1% of ambient surface radiation is present at a depth of 1.6 m. Field studies have indicated that larvae of xanthid crabs are found in greatest abundance at depths which exceed 1.6 m by factors of from 2 to 9 (Bousfield, 1965; Dudley and Judy, 1971; Sandifer, 1973).

It thus appears that proper experimental procedure requires the use of very low intensities. A range of from 10 ft.-c to 70 ft.-c was chosen for this study to meet this criterion. By comparison, it is at the lower end of the range used by Bayne (1964) in his classic study of phototaxis in bivalve larvae.

The positive phototaxis described here for early zoeae of *L. floridanus* and *P. herbstii* confirms the observations reported by Spooner (1933), Foxon (1934), Christenson and McDermott (1958), and Herrnkind (1968) for other species. Specific reports on phototaxis in late zoeae and megalopa are rare. Welsh (1932) found that some larvae became photonegative as development proceeded in the mussel crab *Pinnotheres maculatus*. In contrast, the current study demonstrates

that in the two species tested, late zoeae and the megalopa remain positively phototactic.

Both of the primary orientations reported here have been described by Welsh (1932) and Spooner (1933) for other zoea larvae. Contrary to these earlier reports, however, the present study indicates that the "forward" position illustrated in Figure 2A is most common. The location at the top of the horizontal tank characteristic of the "backward" primary orientation (Figure 2B) suggests that negative geotaxis and positive phototaxis combine in a small per cent of the larvae. When primary orientation is dominated by gravity, movement is upward. After the larvae have reached the top of the horizontal tank, they swim toward the light. The backward movement may be the only orientation possible which permits movement toward the light when the gravity stimulus is dominant.

Fraenkel and Gunn (1961) define "high kinesis" as an increase in activity which results from a high intensity of stimulus. By this definition, the response of first stage zoeae of *P. herbstii* to changes in light intensity can be termed high photokinesis. The comparative insensitivity of larvae of *L. floridanus* illustrates that there may be considerable variability in behavior among larvae of closely related species. The difference between these two species may be due to the apparent higher intrinsic rate of swimming in larvae of *L. floridanus* as compared to *P. herbstii*. *L. floridanus* larvae may be swimming at or near their physical capacity even at low light intensities.

The relative influence of light and gravity as taxis stimuli is of special significance in the megalopa. The dominant positive geotaxis shown by the megalopa is in conflict with the results reported by Rice (1966) for megalopa of *Macropipus sp.* and *Carcinus maenas,* both of which exhibited negative geotaxis. However, the apparent presence in this stage of conflicting orienting stimuli results in a dynamic situation which could cause considerable variation in response among different species. The specific responses of each species may be related to habits of the adult or to specific requirements for metamorphosis.

The author has suggested elsewhere that the responses of larvae of *L. floridanus* and *P. herbstii* to gravity and hydrostatic pressure, combined with characteristic passive sinking rates, provide a mechanism for depth regulation in the absence of light. Laboratory studies suggested that the four zoea stages and the megalopa of each species assume a differential vertical distribution, with succeeding stages showing a deeper net distribution (Sulkin, 1973).

The application of light at low intensities alters this basic pattern considerably. The response varies with each larval stage. While the net vertical distribution of the first zoea stage appears not to be influenced by light, the remaining stages show a much higher per cent of the sample in the upper half of the tank (Table IV).

Although a pattern of differential vertical distribution is retained, the relationships among the larval stages are different. The second and third stages may show a more shallow net distribution than does the first stage, although the fourth zoea stage and the megalopa are deeper. It is apparent, however, that the deeper position of late developmental stages is not due to a change in phototaxis as has been theorized for some other groups of larvae (Thorson, 1964).

Because light is such a variable parameter in the marine environment, its impact upon vertical distribution should be considered supplementary to the pat-

tern shown by crab larvae in the absence of light. The more shallow net distribution of most stages when light is present indicates that an intrinsic mechanism for diurnal vertical migration is present. Experimental evidence thus indicates that larvae should move up toward the surface during the day and gradually disperse downward at night. Such a pattern has been reported in field studies of larvae of the lobster *Homarus americanus* (Templeman and Tibbo, 1945).

By scattering vertically, meropelagic larvae may encounter horizontal currents moving in different directions at different depths, thus increasing the potential for dispersal. Differential vertical distribution through ontogeny provides an intrinsic mechanism for enhancing vertical scattering during larval development. This study has demonstrated that the response of larvae to light superimposes upon the basic pattern an additional mechanism for vertical scattering; namely, diurnal vertical migration.

SUMMARY

1. Experiments were conducted to determine the phototaxis responses of each larval stage of two species of Xanthid crabs and to assess the influence of light on depth regulation.

2. Two primary orientations in response to light are described.

3. Secondary orientation in response to light results in positive phototaxis in all four zoea stages and the megalopa of each species.

4. In response to changes in light intensity, the first zoea stage of *P. herbstii* demonstrated high photokinesis. Although some increase in swimming rate in response to increased light intensity was noted in larvae of *L. floridanus*, particularly in the first zoea stage, the differences were not statistically significant. It is suggested that larvae of *L. floridanus* may swim at their capacity at low light intensities, in contrast to larvae of *P. herbstii*.

5. Light response dominates that of gravity in the first zoea stage; in the megalopa, gravity response dominates that of light in a majority of individuals.

6. Light aimed down the axis of the observation tank exerts a negligible effect upon the net vertical distribution of the first zoea stage. However, the net distribution of later larval stages is shallower in light than is the case in darkness.

7. The response of the larvae to light thus superimposes diurnal vertical migration upon the basic pattern of differential vertical distribution through ontogeny. These two characteristics of larval development will result in considerable vertical scattering during the dispersal phase.

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